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Phytochrome gene diversity

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ABSTRACT

The structures and functions of the phytochrome apoprotein genes (the *PHY* genes), their diversity across the plant kingdom, and their evolution are central concerns in the study of red-light sensing in plants. We summarize here recent advances in two areas relating to these topics: (1) the characteristics of the *PHY* gene family in *Arabidopsis thaliana*, the higher plant species for which the most extensive information on these genes is available, and (2) the similarity relationships, phylogeny, and evolutionary implications of *PHY* gene sequences and partial sequences which have been described from various plants. Together, these two areas of study, one directed at understanding in detail the phytochromes present in a single species and the other directed at a much broader understanding of *PHY* gene relatedness and distribution, are producing an increasingly clear picture of the diversity and evolution of plant red-light photoreceptors. Moreover, they suggest that the complexity of the phytochrome family has increased as land plants have evolved novel morphologies.

Key-words: *Arabidopsis thaliana*; multigene family; nuclear gene phylogeny; phytochrome evolution; plant photoreceptor.

THE ARABIDOPSIS PHYTOCHROME GENE FAMILY

Arabidopsis *PHY* gene structures

Sharrock & Quail (1989) and Clack, Mathews & Sharrock (1994) described five phytochrome coding regions derived from Arabidopsis cDNA sequences and designated them *PHYA*, *B*, *C*, *D* and *E*. Comparison of the deduced protein sequences of the five phytochromes indicates that four divergent types are encoded, the phyA, phyB/D, phyC and phyE types, while the phyB and phyD proteins are clearly a more closely related subgroup. The phylogenetic analysis of *PHY* sequences described later in this review addresses more extensively the sequence relationships and possible evolutionary origins of these various receptor types and generally supports the contention that Arabidopsis is representative of other flowering plants in terms of its *PHY* gene content. The possibility that additional *PHY* genes, beyond *PHYA–E*, are present in the Arabidopsis genome cannot be discounted, but low-stringency hybridization and degenerate primer PCR analyses have not uncovered any evidence for this (R. Sharrock, unpublished results). The five *PHY* genes have been mapped to four of the five Arabidopsis chromosomes, with the *PHYD* and *PHYE* genes both located on chromosome 4 but 5–10 cM apart (R. Sharrock, unpublished results).

Figure 1 shows the structures of the five *PHY* genes. Intron number and location are highly conserved, with two notable exceptions. All of the genes contain two short introns at homologous positions which divide the genes into coding exons I, II and III in the figure. Four of the five contain a third intron, producing coding exon IV, but this intron is missing in *PHYC* (Cowl *et al.* 1994). Multiple transcription start sites for the *PHYA* gene have been mapped and the 5' untranslated region has been shown to contain a large intron (Dehesh *et al.* 1994). For the other *PHY* transcripts, lower limits to the 5' ends are known from cDNA and 5' RACE sequences (Sharrock & Quail 1989; Clack *et al.* 1994) and, as yet, no evidence for multiple start sites or for a 5' untranslated-region intron in any of the other genes has been reported. Primer extension and S1 nuclease protection analysis of the *PHYD* and *PHYE* 5' ends (R. Sharrock, unpublished results) indicate that the transcription start sites for these genes are likely to be close to the 5' RACE products already described. Hence, though in the absence of definitive mapping of the 5' ends of *PHYB–E* it is not possible to draw final conclusions, it appears that each of the three most divergent phytochrome gene lineages – *PHYA*, *PHYB/D/E* and *PHYC* (see Fig. 2 in the following section) – is distinguished by the presence or absence of specific introns (Fig. 1). Other molecular characteristics shared by the Arabidopsis *PHY* genes and shown in Fig. 1 include the presence of multiple short upstream open reading frames (URFs) in the 5' untranslated regions and the use of multiple poly(A) addition sites in at least *PHYA* and *PHYB* (Sharrock & Quail 1989; Clack *et al.* 1994).

Arabidopsis *PHY* gene expression and function

The five Arabidopsis *PHY* genes are expressed at both the mRNA (Clack *et al.* 1994) and protein (Somers *et al.* 1991; J. Tepperman, P. Quail & R. Sharrock, unpublished results) levels, yielding products of the sizes predicted from gene and cDNA sequences. These gene products are present throughout most stages of plant development and in most plant organs, indicating that, at least to a first approximation, the red-light photoreceptor types overlap

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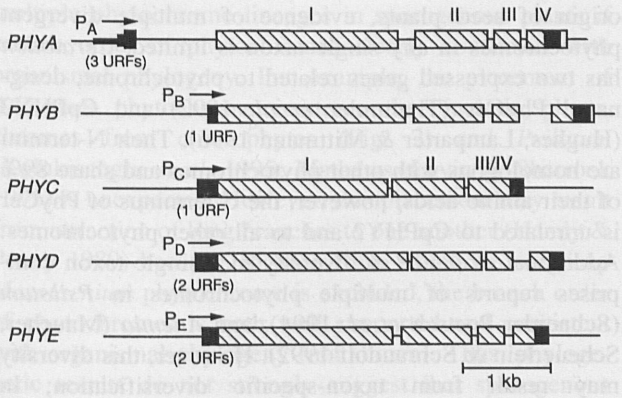

Figure 1. Structures of the five Arabidopsis *PHY* genes. Genomic DNA sequences of *PHYA* (Dehesh *et al.* 1994), *PHYB* (Reed *et al.* 1993), *PHYC* (Cowl *et al.* 1994), *PHYD* and *PHYE* (T. Clack & R. Sharrock, unpublished results) and the corresponding cDNA sequences (Sharrock & Quail 1989; Clack *et al.* 1994) were used to deduce gene structures. Untranslated regions at the 5' and 3' ends of the transcripts are shown in black or white and coding regions are stippled. The number of upstream open reading frames (URFs) present in the 5' untranslated region of each gene is noted and occurrence of multiple poly(A) addition sites is indicated by a white box in the 3' untranslated region.

extensively in terms of their locations within the plant and constitute a very generally distributed antenna for light. Translational fusions of 2–2·5 kb 5' upstream regions of the *PHYA*, *B*, *D* and *E* genes to the GUS coding sequence have been introduced into Arabidopsis (Somers & Quail 1995a,b; L. Palecanda, L. Wester & R. Sharrock, unpublished results). The patterns of GUS fluorometric activity and histochemical staining in these transgenic plants confirm that, while there are some distinct differences in the developmental and tissue-specific controls on the activities of these four promoter regions, they are active in fairly general and highly overlapping patterns.

The individual functions of three of the Arabidopsis *PHY* genes have been identified by isolation of null mutations in these genes. Mutants lacking phyA exhibit loss of far-red light (FR) high irradiance control of hypocotyl elongation, cotyledon expansion and seed germination while mutants lacking phyB show alteration in shade avoidance responses including the effects of red light (R) and of the R:FR ratio on hypocotyl elongation, flowering time and leaf morphology (reviewed in Smith 1995). Aukerman *et al.* (1997) describe a null mutation in the *PHYD* gene found as a naturally occurring allele in the Wassilewskija (Ws) ecotype of Arabidopsis. Loss of phyD causes alteration of many of the same shade avoidance responses which are affected in the *phyB* mutant, but comparison of the two null mutants shows that phyB plays a much more prominent role than phyD. Hence, diversification of the *PHY* gene family, at least in the case of the dicot plant Arabidopsis, has allowed the evolution of distinct photosensory roles for the photoreceptor subfamilies, with the most divergent genes, exemplified by *PHYA* and *PHYB*, having highly divergent functions and the most closely related genes, *PHYB* and *PHYD*, having overlapping or even somewhat redundant roles. Mutants lacking phyC or phyE have not been described and their functions therefore remain to be determined.

DIVERSIFICATION OF THE PHYTOCHROME GENE FAMILY DURING THE EVOLUTION OF PLANTS

The origin of phytochrome

The most ancestral phytochrome that has been fully characterized is that of the green alga *Mesotaenium* (Lagarias, Wu & Lagarias 1995; Wu & Lagarias 1997, this volume). Evidence of homologues in prokaryotes is limited, though similarity among the C-termini of phytochromes and the histidine kinase domains of bacterial two-component response regulators has been noted (e.g. Schneider-Poetsch *et al.* 1991). The strongest support for common ancestry comes from characterization of a phytochrome-like putative photoreceptor from the cyanobacterium *Fremyella* (Kehoe & Grossman 1996) and from sequence analysis of the genome of *Synechocystis* strain PCC 6803 (Kaneko *et al.* 1995). The sequence from *Fremyella*, RcaE, comprises a C-terminus with motifs characteristic of histidine kinase domains and an N-terminus that is weakly similar to the chromophore-binding domain of phytochrome. *Synechocystis* sequence 1001165 (accession D64001) is more similar to phytochrome than is RcaE but, while striking, the degree to which the likeness reflects homology remains unclear because the pattern of similarity among phytochromes and sequences from *Synechocystis* suggests that the chromophore domain and the C-termini of phytochromes have different evolutionary histories. For example, an additional sequence (1001288, accession D64003) from *Synechocystis* has a putative chromophore-binding domain that is more similar to phytochromes than is RcaE, but the C-terminus is similar to a different class of response regulators, exemplified by PleD (Hecht & Newton 1995) from *Caulobacter* (S. Mathews, unpublished results). In addition, the direct repeat in the hinge region of phytochrome may be related to yet other bacterial molecules (Lagarias *et al.* 1995). Thus, further data are needed to confirm the relationship of phytochromes with specific prokaryotic molecules.

PHY gene diversity in land plants

During land plant evolution, phytochromes have diversified from a single progenitor into multiple related lineages or subfamilies. Here, we evaluate and review their sequence relationships and evolution by phylogenetically analysing all available full-length phytochromes and two partial sequences using neighbour-joining and parsimony algorithms in PAUP* (Swofford 1996). Additional *PHY* gene sequence fragments were not included because, for the most part, they result in phylogenies that are not robust to changes in rooting or method of analysis (e.g.

Kolukisaoglu *et al.* 1995; S. Mathews, unpublished results) and therefore provide little further insight. Results shown in Fig. 2 are from analysis of homologous amino acids rather than nucleotides because the divergence (nucleotide substitutions per site) between many sequence pairs is > 1. Trees were rooted by designating a phytochrome sequence from an ancestral taxon, the green alga *Mesotaenium*, as the outgroup (Maddison, Donoghue & Maddison 1984), and support for phylogenetic groups was evaluated by bootstrap resampling (Felsenstein 1985). We addressed the following questions: (1) what is the mode of phytochrome evolution in land plants, and (2) what are the relationships of phytochromes from sporogenous plants and gymnosperms to phytochrome subfamilies in flowering plants?

In sporogenous plants, which diversified before the origin of seed plants, evidence of multiple divergent phytochromes in any single taxon is limited. *Ceratodon* has two expressed genes related to phytochrome, designated PhyCer (Thummler *et al.* 1992) and CpPHY2 (Hughes, Lamparter & Mittmann 1996). Their N-termini are homologous with other phytochromes and share 89% of their amino acids; however, the C-terminus of PhyCer is unrelated to CpPHY2 and to all other phytochromes. Additional evidence of diversity in a single taxon comprises reports of multiple phytochromes in *Psilotum* (Schneider-Poetsch *et al.* 1994), and *Anemia* (Maucher, Scheuerlein & Schraudolf 1992). However, this diversity may result from taxon-specific diversification; in *Psilotum,* it may reflect a highly duplicated genome. Phylogenetic analyses could suggest the presence of

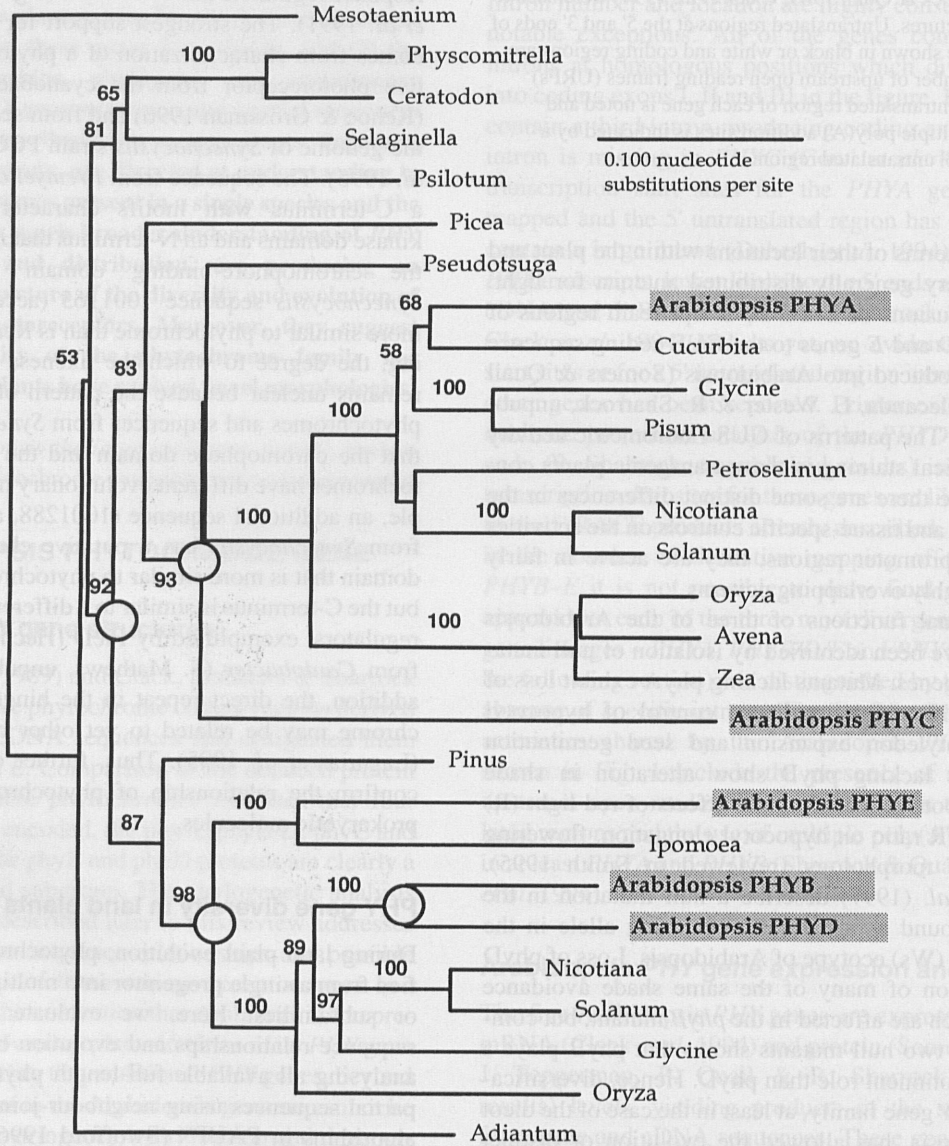

Figure 2. Neighbour-joining tree of phytochrome amino acid sequences. Open circles represent gene duplications. Distances in nucleotide substitutions per site are indicated by branch lengths relative to the scale of 0·100 substitutions per site shown. Values from 100 bootstrap replicates are given above branches.

multiple phytochrome lineages in sporogenous plants if branch order of phytochromes clearly conflicted with organismal phylogeny. For example, the placement of *Adiantum* phytochrome in trees that include phytochromes from chlorophytes (Fig. 2) and *Psilotum* (Kolukisaoglu *et al.* 1995; Mathews, Lavin & Sharrock 1995) is unexpected. However, this placement may result from attraction of long branches to one another (Hendy & Penny 1989) because, in trees from which the outgroup *Mesotaenium* phytochrome is excluded, the branch order of phytochromes is both well supported and consistent with organismal phylogeny (not shown). Thus, phylogenetic results do not strongly suggest that sporogenous plants have, or had, more than one phytochrome subfamily. Moreover, they suggest no well-supported relationship of phytochromes from sporogenous plants with individual seed plant *PHY* subfamilies.

The presence of multiple phytochrome genes in individual species of seed plants is well established, and phylogenetic analyses indicate that, following the major duplication events, these genes have been evolving independently (e.g. high bootstrap values in Fig. 2 and in Mathews *et al.* 1995). As shown in Fig. 2, the earliest gene duplication gave rise to the lineage comprising homologues of Arabidopsis *PHYA* and *PHYC* on the one hand and the lineage comprising homologues of Arabidopsis *PHYE* and *PHYB/D* on the other. Subsequent duplications resulted in the divergence of *PHYA* from *PHYC* and of *PHYE* from *PHYB/D*. Divergence of *PHYB* from *PHYD* in Arabidopsis followed a recent duplication. This evolutionary pattern is consistent with the functional divergence among phytochromes in flowering plants reviewed in the section 'Arabidopsis *PHY* gene expression and function' above. Furthermore, it is notable that the earliest three diversification events in the phytochrome gene family may have occurred at or near major morphological transitions that mark the evolution of plants: the *PHYA/C–PHYB/D/E* duplication near the origin of seed plants and the *PHYA–PHYC* and *PHYB/D–PHYE* duplications near the origin of flowering plants.

At least two of the phytochrome lineages known from flowering plants appear to have been established before the divergence of conifers from other gymnosperms (Fig. 2). For example, the sequence from *Pinus* is most closely related to the *PHYB/D/E* subfamily, while the sequence from *Picea* is most closely related to the *PHYA/C* subfamily. Furthermore, *Pseudotsuga* phytochrome does not cluster with *Picea* phytochrome, as we would expect of homologous sequences from closely related taxa, so it is possible that the phytochrome gene family in conifers comprises three divergent lineages. This interpretation is consistent with the observation that *PHYA*, *PHYB/D/E* and *PHYC* are well separated from one another in the earliest flowering plants (Kolukisaoglu *et al.* 1995; S. Mathews, unpublished results), with the position of the phytochrome fragment from the gymnosperm *Ephedra* as sister to *PHYA*s (Kolukisaoglu *et al.* 1995), and with the suggestion that two unpublished sequences from pine are *PHYA*- and *PHYC*-like (Quail 1991). Together, these observations suggest that three of the four major flowering plant phytochrome lineages may be homologous with phytochromes found in gymnosperms.

Phytochrome lineages in flowering plants

Phytochrome genes have been detected in all major subclasses of flowering plants. Figure 3 summarizes results of phylogenetic analyses of 172 full or partial sequences in GenBank. Data were either partitioned according to sequence length or combined in a matrix in which absent nucleotides were coded as missing data. Each of the sequences belongs unequivocally (91% or higher bootstrap support) to one of the four phytochrome lineages identified in analysis of full-length sequences: *PHYA*, *PHYB/D*, *PHYC* or *PHYE*. Three of these four gene lineages occur widely in flowering plants but, to date, homologues of *PHYE* have not been detected in monocots (Mathews *et al.* 1995; Mathews & Sharrock 1996; S. Mathews, unpublished results). This distribution could result from the divergence of *PHYE* from *PHYB/D* having occurred after the divergence of monocots from dicots or from *PHYE* being lost from monocots. There is currently no DNA sequence data suggesting the presence

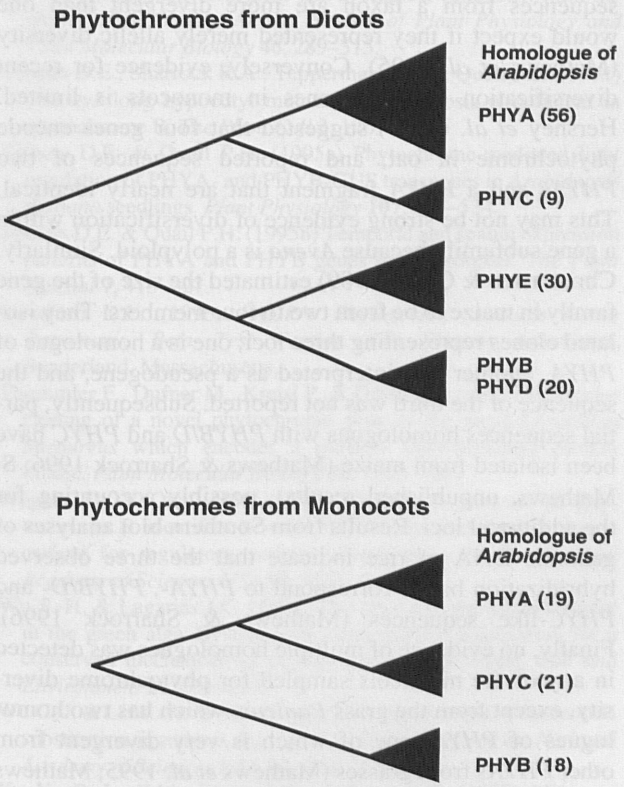

Figure 3. Distribution and relationships of 172 complete or partial phytochrome nucleotide sequences from flowering plants. Numbers in parentheses represent the number of sequences sampled from GenBank; tomato *PHYF* occurs in the *PHYC* clade.

of additional, widely distributed phytochrome lineages in flowering plants. In our analysis, tomato *PHYF* (Hauser *et al.* 1995) is a member of the well-supported (91% bootstrap value) cluster including eight *PHYC* homologues from dicots (Fig. 3). The interpretation of *PHYF* as a novel *PHY* subfamily (Hauser *et al.* 1995) was based on the degree of divergence between Arabidopsis *PHYC* and tomato *PHYF* and assumes that rates of nucleotide substitution among phytochrome subfamilies are equal. However, evidence is presented below that the *PHYC* subfamily is in fact diverging in sequence faster than the *PHYA* and *PHYB* subfamilies. Reports of additional genes in tomato (total of 9–12) inferred from Southern analyses (Hauser *et al.* 1995) have not been substantiated with sequence data. The possibility remains that such very high diversity may be the result of recent duplications within the *PHY* gene family in *Solanum*, or in some larger taxonomic group to which tomato belongs.

Recent diversification in the gene family is evident within dicot flowering plants, exemplified by gene duplications in the *PHYA* and *PHYB/D* subfamilies. Multiple homologues of *PHYB/D* are found in Arabidopsis, carrot and tomato, while multiple homologues of *PHYA* are found in carnation, legumes and *Ceratophyllum*, an aquatic angiosperm (Mathews *et al.* 1995). In legumes, the duplicate *PHYA*s form a discrete lineage that is derived from within their *PHYA* subfamily (Mathews *et al.* 1995; Lavin *et al.*, 1997). In all cases, multiple sequences from a taxon are more divergent than one would expect if they represented merely allelic diversity (Mathews *et al.* 1995). Conversely, evidence for recent diversification of *PHY* genes in monocots is limited. Hershey *et al.* (1985) suggested that four genes encode phytochrome in oat, and reported sequences of two *PHYA*s and a *PHYA* fragment that are nearly identical. This may not be strong evidence of diversification within a gene subfamily because *Avena* is a polyploid. Similarly, Christensen & Quail (1989) estimated the size of the gene family in maize to be from two to four members. They isolated clones representing three loci; one is a homologue of *PHYA*, another was interpreted as a pseudogene, and the sequence of the third was not reported. Subsequently, partial sequences homologous with *PHYB/D* and *PHYC* have been isolated from maize (Mathews & Sharrock 1996; S. Mathews, unpublished results), possibly accounting for the additional loci. Results from Southern blot analyses of genomic DNA of rice indicate that the three observed hybridization bands correspond to *PHYA*-, *PHYB/D*- and *PHYC*-like sequences (Mathews & Sharrock 1996). Finally, no evidence of multiple homologues was detected in any of the monocots sampled for phytochrome diversity, except from the grass *Panicum* which has two homologues of *PHYA*, one of which is very divergent from other *PHYA*s from grasses (Mathews *et al.* 1995; Mathews & Sharrock 1996).

At the nucleotide level, diversification in the *PHY* gene family in flowering plants is characterized by unequal rates of divergence. Relative rates of non-synonymous nucleotide substitution between all currently available full-length *PHY* coding sequences and the reference *PHY* sequence from *Selaginella* were determined (Mathews *et al.* 1995; Mathews & Sharrock 1996; S. Mathews, unpublished results). Table 1 shows that, in all possible pairwise comparisons of *PHYA* and *PHYB* sequences from single taxa, *PHYA*s are significantly more divergent from the common ancestor than are *PHYB*s. Furthermore, in Arabidopsis where full-length sequences are available, *PHYC* is significantly more divergent compared to *PHYA*, *PHYB* and *PHYD*, while *PHYE* is evolving rapidly relative to *PHYB* and *PHYD* (Table 1). Thus, overall, *PHYB/D* appears to be the most evolutionarily constrained *PHY* sequence, followed by *PHYA*, then *PHYC* and *PHYE*. Differences in the rates of divergence for two full-length phytochrome coding sequences, for instance *PHYA* and *PHYC*, are largely due to differences in the C-terminal half of the molecule. When the data are partitioned by exon (see Fig. 1 for exon structure), nucleotide substitution is more highly constrained in exons I, III and IV and is least constrained in exon II (data not shown). It has been proposed from mutational studies that sequences coded in exon II are critical for phytochrome's regulatory activity (Wagner & Quail 1995; Xu *et al.* 1995) so it is possible that rapid evolution of *PHYC* and *PHYE* in this region reflects functional divergence.

Table 1. Results from pairwise comparisons of relative rates of nucleotide substitutions (Wu & Li 1985) among full-length *PHY* sequences. The value d_{13}-d_{23} is the difference in non-synonymous nucleotide substitutions between sequence 1 and sequence 2 relative to reference sequence 3, *Selaginella PHY*. SE is the standard error; single asterisks indicate differences significant at the 0·05 level and double asterisks differences at the 0·01 level. At = Arabidopsis, Nt = *Nicotiana*, St = *Solanum*, Os =*Oryza*, Gm = *Glycine*

Seq 1	Seq 2	d_{13}-d_{23}	SE	Direction
At A	At B	0·0454*	±0·0183	(A>B)
At A	At C	–0·0429*	±0·0202	(C>A)
At A	At E	–0·0242	±0·0198	
At B	At C	–0·0883**	±0·0254	(C>B)
At B	At E	–0·0696**	±0·0189	(E>B)
At C	At D	0·0770**	±0·0194	(C>D)
At C	At E	0·0187	±0·0207	
At D	At E	–0·0583**	±0·0191	(E>D)
Os A	Os B	0·0732**	±0·0188	(A>B)
Nt A	Nt B	0·0962**	±0·0176	(A>B)
St A	St B	0·0786**	±0·0181	(A>B)
Gm A	Gm B	0·0403*	±0·0192	(A>B)

GenBank accession numbers of the sequences we analysed are X75025, X17084, X61458, D13519, X74931, X74930, X17342, L10114, S51538, X76609, X76610,X57563, X03242, X14172, P19862, X17341, M15265, M37217, X66784, S84872, X17343, U22458, U39787, L34843, L34844, X75412, U56698, U31284, X96738, U60264, U08142-U08184 and U61185-U61220.

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REFERENCES

Aukerman M.J., Hirschfeld M., Wester L., Weaver M., Clack T., Amasino R.M. & Sharrock R.A. (1997) A deletion in the *PHYD* gene of the Arabidopsis Wassilewskija ecotype defines a role for phytochrome D in red/far-red light sensing. *The Plant Cell*, in press.

Christensen A.H. & Quail P.H. (1989) Structure and expression of a maize phytochrome-encoding gene. *Gene* **85**, 381–390.

Clack T., Mathews S. & Sharrock R.A. (1994) The phytochrome apoprotein family in *Arabidopsis* is encoded by five genes: the sequences and expression of *PHYD* and *PHYE*. *Plant Molecular Biology* **25**, 413–427.

Cowl J.S., Hartley N. Xie D.-X., Whitelam G.C., Murphy G.P. & Harberd N.P. (1994) The *PHYC* gene of *Arabidopsis*. *Plant Physiology* **106**, 813–814.

Dehesh K., Franci C., Sharrock R.A., Somers D.E., Welsch J.A. & Quail P.H. (1994) The *Arabidopsis* phytochrome A gene has multiple transcription start sites and a promoter sequence motif homologous to the repressor element of monocot phytochrome A genes. *Photochemistry and Photobiology* **59**, 379–384.

Felsenstein J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791.

Hauser B.A., Cordonnier-Pratt, M.-M., Daniel-Vedele F. & Pratt L.H. (1995) The phytochrome gene family in tomato includes a novel subfamily. *Plant Molecular Biology* **29**, 1143–1155.

Hecht G.B. & Newton A. (1995) Identification of a novel response regulator required for the swarmer-to-stalked-cell transition in *Caulobacter crescentus*. *Journal of Bacteriology* **177**, 6223–6229.

Hendy M.D. & Penny D. (1989) A framework for the quantitative study of evolutionary trees. *Systematic Zoology* **38**, 297–309.

Hershey H.P., Barker R.F., Idler K.B., Lissemore J.L. & Quail P.H. (1985) Analysis of cloned cDNA and genomic sequences for phytochrome: amino acid sequences for two gene products expressed in etiolated *Avena*. *Nucleic Acids Research* **1**, 8543–8559.

Hughes J.E., Lamparter T. & Mittmann F. (1996) CpPHY2 (PHYCER2), a 'normal' phytochrome in *Ceratodon* (Accession No. U56698) (PGR96–067). *Plant Physiology* **112**, 446.

Kaneko T., Tanaka A., Sato S., Kotani H., Sazuka T., Miyajima N., Sugiura M. & Tabata S. (1995) Sequence analysis of the genome of the unicellular cyanobacterium *Synechocystis* sp. Strain PCC 680. Sequence features in the 1 Mb region from map positions 64% to 92% of the genome. *DNA Research* **2**, 153–166.

Kehoe D.M. & Grossman A.R. (1996) Similarity of a chromatic adaptation sensor to phytochrome and ethylene receptors. *Science* **273**, 1409–1412.

Kolukisaoglu H.U., Marx S., Wiegmann C., Hanelt S. & W.Schneider-Poetsch H.A. (1995) Divergence of the phytochrome gene family predates angiosperm evolution and suggests that *Selaginella* and *Equisetum* arose prior to *Psilotum*. *Journal of Molecular Evolution* **41**, 329–337.

Lagarias D.M. Wu, S.-H. & Lagarias J.C. (1995) Atypical phytochrome gene structure in the green alga *Mesotaenium caldariorum*. *Plant Molecular Biology* **29**, 1127–1142.

Lavin M., Eshbaugh E. Hu J.-M. & Sharrock R.A. (1997) Monophyletic subgroups of the tribe Millettieae (Leguminosae) as revealed by phytochrome nucleotide sequence data. *American Journal of Botany*, in press.

Maddison W.P., Donoghue M.J. & Maddison D.R. (1984) Outgroup analysis and parsimony. *Systematic Zoology* **33**, 83–103.

Mathews S., Lavin M. & Sharrock R.A. (1995) Evolution of the phytochrome gene family and its utility for phylogenetic analyses of angiosperms. *Annals of the Missouri Botanical Garden* **82**, 296–321.

Mathews S. & Sharrock R.A. (1996) The phytochrome gene family in grasses (Poaceae): a phylogeny and evidence that grasses have a subset of the loci found in dicot angiosperms. *Molecular Biology and Evolution* **13**, 1141–1150.

Maucher H.P., Scheuerlein R. & Schraudolf H. (1992) Detection and partial sequence of phytochrome genes in the ferns *Anemia phyllitidis* (L.) Sw. (Schizaeaceae) and *Dryopteris filix-mas* L. (Polypodiaceae) by using the Polymerase-chain reaction technology. *Photochemistry and Photobiology* **56**, 759–763.

Quail P.H. (1991) Phytochrome: a light-activated molecular switch that regulates plant gene expression. *Annual Review of Genetics* **25**, 389–409.

Reed J.W., Nagpal P., Poole D.S., Furuya M. & Chory J. (1993) Mutations in the gene for red/far-red light receptor phytochrome B alter cell elongation and physiological responses throughout *Arabidopsis* development. *The Plant Cell* **5**, 147–157.

Schneider-Poetsch H.A.W., Braun B., Marx S. & Schaumburg A. (1991) Phytochromes and bacterial sensor proteins are related by structural and functional homologies. *FEBS Letters* **281**, 245–249.

Schneider-Poetsch H.A.W., Marx S., Kolukisaoglu H., Hanelt S. & Braun B. (1994) Phytochrome evolution: phytochrome genes in ferns and mosses. *Physiologia Plantarum* **91**, 241–250.

Sharrock R.A. & Quail P.H. (1989) Novel phytochrome sequences in *Arabidopsis thaliana*: structure, evolution, and differential expression of a plant regulatory photoreceptor family. *Genes and Development* **3**, 1745–1757.

Smith H. (1995) Physiological and ecological function within the phytochrome family. *Annual Review of Plant Physiology and Plant Molecular Biology* **46**, 289–315.

Somers D.E., Sharrock R.A., Tepperman J.M. & Quail P.H. (1991) The *hy3* long hypocotyl mutant of Arabidopsis is deficient in phytochrome B. *The Plant Cell* **3**, 1263–1274.

Somers D.E. & Quail P.H. (1995a) Phytochrome-mediated light regulation of PHYA- and PHYB-GUS transgenes in *Arabidopsis thaliana* seedlings. *Plant Physiology* **107**, 523–534.

Somers D.E. & Quail P.H. (1995b) Temporal and spatial expression patterns of PHYA and PHYB genes in Arabidopsis. *The Plant Journal* **7**, 413–427.

Swofford D.L. (1996) *PAUP*: Phylogenetic Analysis Using Parsimony, Beta Test Version 4·0*. Sinauer Associates, Sunderland, Massachusetts.

Thummler F., Dufner M., Kreisl P. & Dittrich P. (1992) Molecular cloning of a novel phytochrome gene of the moss *Ceratodon purpureus* which encodes a putative light-regulated protein kinase. *Plant Molecular Biology* **20**, 1003–1017.

Wagner D. & Quail P.H. (1995) Mutational analysis of phytochrome B identifies a small COOH-terminal-domain region critical for regulatory activity. *Proceedings of the National Academy of Sciences USA* **92**, 8526–8600.

Wu S.-H. & Lagarias J.C. (1997) The phytochrome photoreceptor in the green alga *Mesotaenium caldariorum:* implication for a conserved mechanism of phytochrome action. *Plant, Cell and Environment* **20**, 691–699.

Wu C.-I. & Li W.-H. (1985) Evidence for higher rates of nucleotide substitution in rodents than in man. *Proceedings of the National Academy of Sciences USA* **82**, 1741–1745.

Xu Y., Parks B.M., Short T.W. & Quail P.H. (1995) Missense mutations define a restricted segment in the C-terminal domain of phytochrome A critical to its regulatory activity. *The Plant Cell* **7**, 1433–1443.

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